WINTER FORAGING BEHAVIOR AND PREY SELECTION OF THE SEMIPALMATED PLOVER IN COASTAL VENEZUELA

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ABSTRACT.—We studied wintering Semipalmated Plovers (*Charadrius semipalmatus*) in a mangrove and open bay site in coastal Venezuela to determine whether the minor sexual dimorphism in bill and tarsus lengths in this species was correlated with sexual differences in habitat use, behavior during foraging, and diet. We found no significant differences between the sexes in either habitat use on the mudflats or distances to conspecifics. Neither sex exhibited territorial behavior. Males used significantly more shallow pecks than did females, who used more repetitive probing, particularly at the open bay site. Diets differed between the sexes in the relative abundance of prey in the fecal samples in both habitats, with samples from males containing significantly more dipteran larvae and samples from females containing more copepods and bivalves. Prey size did not vary between the sexes. We documented significant site differences in habitat use, foraging behavior, and diet, probably as a result of differences in prey availability. *Received 10 March 2000, accepted 6 July 2000.*

Few researchers in the tropics have examined the foraging behavior and diet of Neotropical migrant shorebirds, even though overwintering food intake may be an important determinant of survivorship for these birds (Baker and Baker 1973, Schneider 1985, Mercier and McNeil 1994). Foraging behavior and diet in shorebirds can vary as a result of quality of the habitat (Tsipoura and Burger 1999) as well as sexual differences (Durell et al. 1993). Semipalmated Plovers *(Charadrius semipalmatus)* are generalist foragers that feed on small invertebrates, primarily in coastal habitats (Baker and Baker 1973, Skagen and Oman 1996). On the wintering grounds Semipalmated Plovers forage on tidal mud flats that contain a diversity of invertebrate prey (Robert et al. 1989). Semipalmated Plovers exhibit mixed sexual dimorphism: females are 3.7% heavier than males and have proportionately longer wings, but males have bills that are 2% longer than those of females (means of 12.06 mm, 11.85 mm, respectively) and toes that are 2.5% longer than those of females (means of 17.27 mm, 16.84 mm respectively; Teather and Nol 1997).

In other shorebirds the sex with the longer bill can probe more deeply into the substrate for prey than the sex with the shorter bill and can also feed on larger prey (Jonsson and Alerstam 1990). We expected that males, the sex with the longest bill in this species, might forage more frequently on larger prey species and those that occur deeper in the substrate than females. We also expected that males, as a result of their slightly longer toes, might forage more often on softer, wetter substrates, closer to the waterline than females. We tested these predictions by documenting habitat use, foraging behavior, and diet through the use of fecal analyses (Ward 1989, Dekinga and Piersma 1993, Moreira 1994) at two sites (a mangrove and open bay mudflat) in coastal Venezuela (Robert and McNeil 1989).

METHODS

The study was conducted in northeastern Venezuela on the tidal mud flats of the Chacopata Lagoon complex (10° 41′ N, 63° 46′ W), on the northern side of the Araya Peninsula, during October 1997. The lagoon complex consists of many shallow, salt-water bays, rimmed by mangrove swamps and gradually sloping mud-flats. Tidal amplitude in the area is relatively low (averaging only 30 cm), but because of a shallow slope, the mud flats can extend up to 80 m from high to low tide marks (Mercier and McNeil 1994).

The mangrove study site was surrounded by mangrove stands, with approximately 10 m between the high and low tide lines and about 1 km of shoreline. The open bay study site had approximately 4 km of shoreline, was bound by small mangrove stands on two sides, and had 50 m of mudflat exposed at low tide. Because of its greater tidal flushing, the open bay had frequent rafts of decomposing algae wash up on shore at high tide that were not present at the mangrove site.

Semipalmated Plover abundance was at its yearly peak in October (Mercier and McNeil 1994). We sexed birds by the color of their auricular plumage; in females these feathers are the same brown as their backs but in males the feathers are black (Teather and Nol

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1997). Juveniles were distinguished from adults by the presence of buff edges on their wing coverts and solid black bills (Prater et al. 1977). Any adult with ambiguous markings or juvenile was rejected for study (5–10% of the total sample). There was no change in the proportion of birds that we were able to sex or age during the study period.

Feeding substrates were classified with respect to moisture level into one of three categories: dry if above the high tide mark or indistinguishable from areas above the high tide line; damp if there was a noticeable discoloration of the mud or sand as a result of residual water; or wet if a visible film of water remained on the surface. Semipalmated Plovers in our study area were not seen foraging in standing water.

Plovers used two distinct foraging techniques. The first (and most common) was a brief peck into the substrate. The second technique involved a repetitive hammering or probing of the bill into the substrate up to a depth equal to the length of the bill. Both techniques were used by males and females on all substrate types. The two techniques were easily distinguished. Pecking and probing were recorded as single foraging events.

We recorded the behavior of foraging individuals during 5 min observation periods. For each foraging bout the substrate wetness was recorded. We also recorded the distance from the water line for each foraging individual. At the end of 5 min, the species of the closest foraging bird and its distance to the focal individual (estimated as 0–0.9 m, 1–2.9 m, 3–4.9 m, and >5 m) were also recorded.

Data were collected on the first individual located each day at each site. The next bird located of the opposite sex was then observed. When flocks of more than 10 birds were present, we limited our observations to three individuals of each sex per day per site. For flocks less than or equal to 10 birds, only a single bird of each sex was observed to avoid repeatedly selecting the same individuals.

All observations were made using a 25× field spotting scope and 8 × 50 binoculars with the sun at the observer's back. All data were checked for normality using JMP™ ver. 3 for the Macintosh. Count data were analysed using log-linear models and cell χ^2 values were used to test for significant deviations from expected diet values. Linear data were analysed using two-way ANOVA with sex and habitat as main effects. These results are presented as means ± SE. Proportion data were arcsin transformed prior to analysis to normalize data.

Fecal samples were opportunistically collected after witnessing their deposition from individuals of known sex. When viewed through a 25× spotting scope, feces were visible on the mud flats up to 30 m away. Samples from ambiguous sources were rejected. The feces were lifted from the substrate, excluding any surrounding mud or sand, and stored in individual sealed containers containing 70% ethanol for subsequent analysis. The samples were well homogenized when examined (1–2 mo after collection) under a variable magnification (8–50×), stereo, dissecting microscope fitted with an ocular scale. The microscope was also fitted with a 35 mm camera to catalogue any items that were difficult to identify immediately. Prey items were identified to class or family using Gosner (1971) and McAlpine and coworkers (1990).

All items in the fecal samples were counted but length was determined only for unbroken, rigid structures, including the rigid parts of individual prey items. Fecal analysis data were pooled into single samples for each combination of sex and site (Swanson et al. 1974).

RESULTS

Foraging Semipalmated Plovers were observed for almost 200 hours. Intraspecific aggression was observed only once when a foraging adult female displaced a juvenile. Semipalmated Plovers were observed feeding among flocks of small sandpipers (*Calidris mauri, C. pusilla, C. minutilla*), within groups of their own species, or alone during the study. The sexes were not different in their respective distances to conspecifics or other sandpipers, but all Semipalmated Plovers foraged more closely to conspecifics than to sandpipers (distances to conspecific neighbors, males: 1.76 ± 0.25 m, $n = 23$; females: 1.96 ± 0.26; $n = 41$; to small sandpipers, males: 2.86 ± 0.86, $n = 11$; females: 3.17 ± 0.51 m, $n = 18$; species effect: $F_{1,80} = 7.41$, $P < 0.01$; sex effect: $F_{1,80} = 0.36$, $P > 0.05$; no significant interaction). Foraging neighbors were conspecifics in 64 of 93 observations (68.8%).

While the mean distances from the waterline were significantly different between the two sites (site effect: $F_{1,125} = 12.97$, $P < 0.001$), they were not significantly different between the sexes (sex effect: $F_{1,1} = 0.009$, $P > 0.05$: mangrove males: 2.1 ± 0.66 m, $n = 15$; females: 0.7 ± 0.2 m, $n = 15$; open bay males: 4.3 ± 0.8 m, $n = 39$; females: 5.7 ± 0.8 m, $n = 60$; no significant interaction).

Males were observed foraging on dry substrates only twice and females were never seen using dry substrates. Both sexes foraged more on wet than moist substrates [wet substrates: 61/84 observations (72.6%), $G = 13.2$, $P < 0.001$], but there was no significant difference between the sexes in the frequencies with which they used a particular substrate [females: 28/41 (68.2%) observations on wet substrate, males: 25/33 (75.7%) on wet sub-
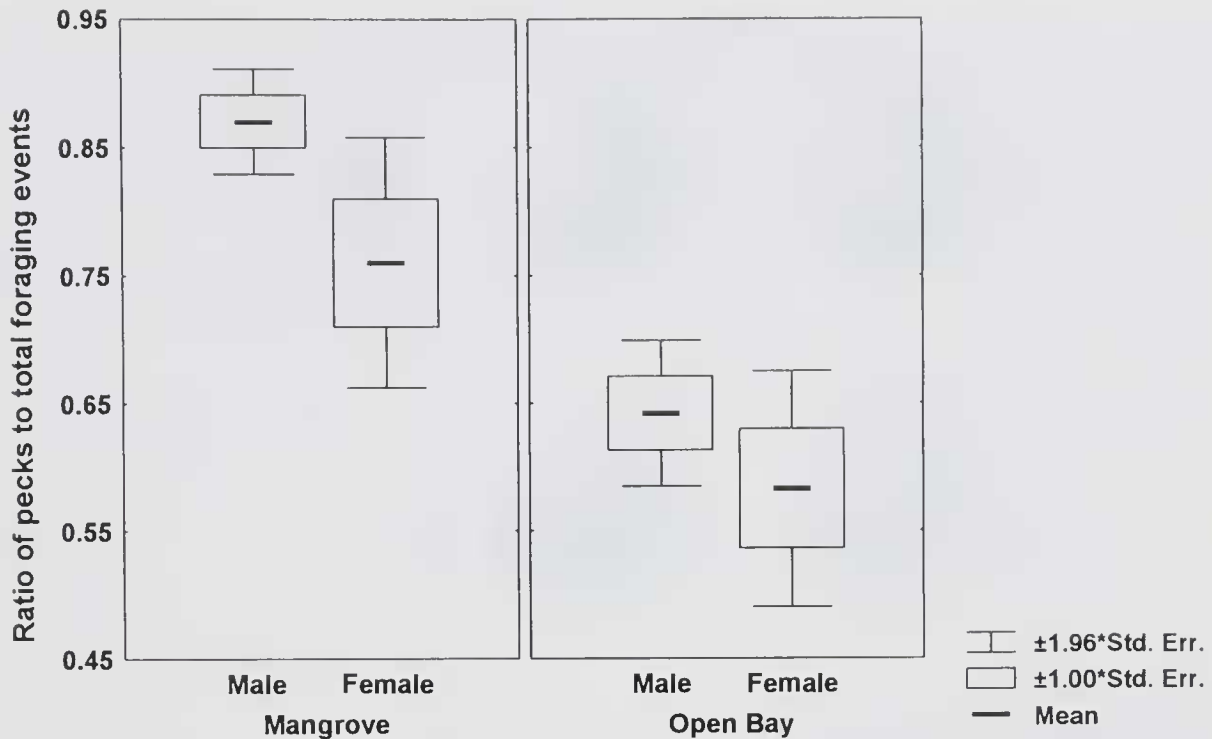
FIG. 1. Ratio of pecks to total foraging events by male and female Semipalmated Plovers on mangrove and open bay mud flats. $1 -$ ratio = proportion of probing events employed during observation period. Males, mangrove, $n = 19$ bouts, females, mangrove, $n = 15$; males, open bay, $n = 24$, females, open bay, $n = 26$.

strate; $G = 1.69$, $P > 0.05$], nor was there a site effect ($G = 0.74$, $P > 0.05$).

Foraging rates for males and females were not significantly different, nor did they vary between habitats (mangrove: males 16.8 ± 1.31 events min^{-1}, $n = 19$; females 15.9 ± 2.22 events min^{-1}, $n = 15$; open bay: males 17.5 ± 0.87 events min^{-1}, $n = 24$; females 16.6 ± 0.89 events min^{-1}, $n = 26$; sex effect: $F_{1,80} = 0.76$, $P > 0.05$; site effect: $F_{1,80} = 0.504$, $P > 0.05$; no significant interaction). The ratio of pecks to the total number of feeding events during the observation period was significantly larger for males than females at both sites, with males using fewer probes than females and both sexes using significantly more pecks (and fewer probes) as a proportion of total foraging events at the mangrove site than at the open bay (sex effect: $F_{1,80} = 4.54$, $P < 0.04$; site effect: $F_{1,80} = 30.8$, $P < 0.001$; no significant interaction; Fig. 1).

Individual and whole prey items were recognizable in the fecal samples, often in great numbers. Adult insects were present in almost all fecal samples (38/39, 97.4%) but were usually too fragmented to count individuals. Bivalve mollusks were the next most common prey item (179 individual prey, 22/30 samples, 56.4%) followed by larvae of flies from the

family Dolichopodidae (long-legged flies; 380 items, 20/39 samples, 51.3%), copepod crustaceans (323 prey, 22/39 samples, 56.4%), adult Corixidae (too fragmented to count individuals, 15/39, 38.5%), and Canacidae fly larvae (74 individual prey, 9/39 samples, 23.1%). Gastropods (137 individuals, 2 samples), amphipods (1 individual, 1 sample), isopods (1 individual, 1 sample), fiddler crabs (*Uca thayeri*; too fragmented to count, 3 samples) and an unidentified shrimp (Decapoda, 1 sample) were of minor importance in the diet.

The number of prey items that occurred in fecal samples did not differ between the sexes [sex effect: $F_{1,35} = 3.49$, $P < 0.07$; analysis performed on log-transformed data; mangrove: males' mean = 15.1 prey items (95% CI: 10.9–21.0), $n = 13$ samples; females' mean = 28.1 (95% CI: 19.4–40.7), $n = 14$, open bay: males' mean = 9.1 (95% CI: 5.6–14.4), $n = 6$; females' mean = 10.1 (95% CI: 6.6–15.5), $n = 6$] but there were significantly more prey items in fecal samples from the mangrove than from the open bay site (site effect: $F_{1,35} = 15.5$, $P < 0.001$; no significant interaction).

None of the prey items that were frequently found and measured in the fecal samples showed any significant differences in size be-
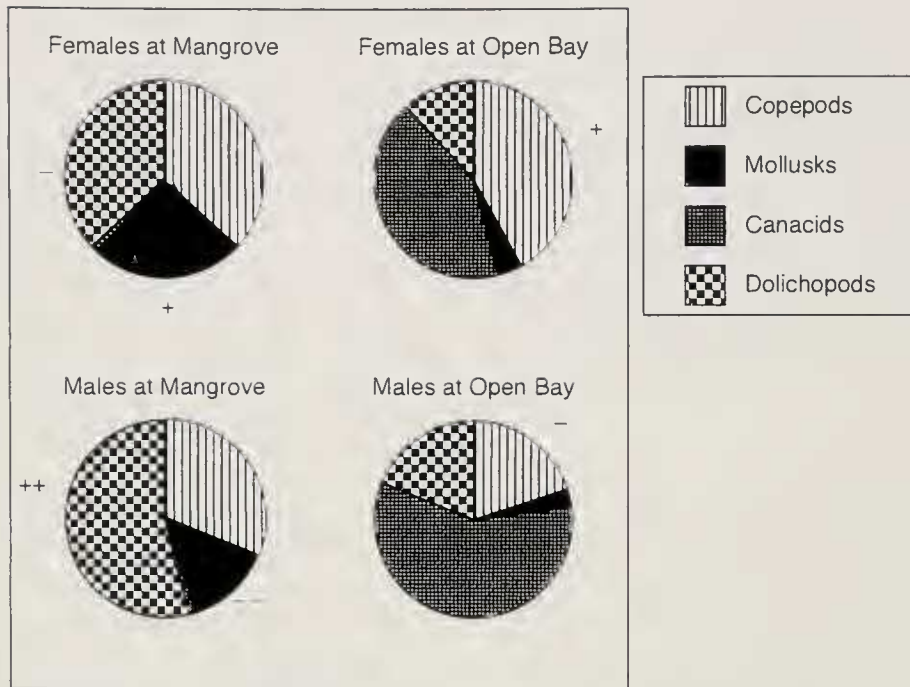
FIG. 2.   Proportions of total prey items of four different prey found in fecal samples from males and females at mangrove and open bay habitats. Samples consist of pooled samples from 13 male (232 prey items) and 14 female (481 prey items) fecal samples from the mangrove site, 6 male (59 prey items) and 6 female (65 prey items) fecal samples from the open bay. + and − indicate largest deviations from expected when comparing the two sexes within a habitat (see text for values).

tween the two sexes [Dolichopodidae larvae (length of cephalopharyngeal skeleton): males, 0.58 ± 0.02 mm, $n = 108$; females, 0.58 ± 0.02 mm, $n = 157$; Canacidae larvae (distance between dorsal and ventral cornu of cephalopharyngeal skeleton): males, 0.053 ± 0.001 mm, $n = 60$; females, 0.052 ± 0.001 mm, $n = 16$; bivalve molluscs (longest axis of shell): males, 0.52 ± 0.02 mm, $n = 45$; females, 0.53 ± 0.02 mm, $n = 126$; copepod crustaceans (body length): males, 0.42 ± 0.01 mm, $n = 111$; females, 0.42 ± 0.02 mm, $n = 21$: t-tests, all comparisons between sexes, $P > 0.05$].

For both sexes, the beach flies (Canacidae larvae) were virtually absent from fecal samples collected from the mangrove habitat, whereas this group of insects formed a numerically important part of the fecal samples at the open bay site (Fig. 2). The long-legged flies (Dolichopodidae) formed a numerically large proportion of the diet for both sexes at the mangrove site. The relative proportions of prey items of different categories found in all fecal samples (combined because little individual variation within sex and habitat group) varied significantly between the sexes both at the mangrove site ($G = 15.9$, $P < 0.001$) and

at the open bay ($G = 13.8$, $P < 0.001$; data from each habitat analyzed separately because of significant interaction between site and sex). The largest contributions to the deviations from expected in this analysis suggested that fecal samples of males foraging at the mangrove site contained more dolichopods (cell $\chi_1{}^2 = 6.16$, $P < 0.05$) and fewer mollusks than expected (cell $\chi_1{}^2 = 7.07$, $P < 0.05$) whereas fecal samples of females at this site contained no significant differences in mollusks (cell $\chi_1{}^2 = 2.97$, $P > 0.05$) or in dolichopods (cell $\chi_1{}^2 = 3.41$, $P > 0.05$; Fig. 2). At the open bay the greatest deviations to the model were from females foraging more on copepods (cell $\chi_1{}^2 = 2.10$, $P > 0.05$) and males less (cell $\chi_1{}^2 = 2.32$, $P > 0.05$) although only the full model was significant. When contrasting the consumption of all fly larvae with hard-shelled prey like copepods and crustaceans, females consumed higher proportions of these prey than males in both habitats [females at mangrove site: 128/311 (41.1%) total prey items consisted of copepods and bivalves, males at mangrove site: 104/402 (25.8%); $G_1 = 18.6$, $P < 0.001$; females at open bay: 45/80 (56.3%) of prey consisted of

copepods and bivalves, males at open bay: 14/44 (31.8%); $G_1 = 6.92$, $P < 0.01$].

DISCUSSION

We found minor differences in the foraging behavior and diet of male and female Semipalmated Plovers that do not seem to be explained by the very small differences in bill length between the sexes. We predicted that males, with their longer bills, might forage on larger prey items than females. We did not find support for this prediction; the mean sizes of the rigid structures of the prey found in the fecal samples were sometimes identical.

The behavioral differences in foraging that we documented appeared opposite in direction to our prediction; females were more likely to use probing than were males, the method that appeared to result in deeper penetration into the substrate by the bill. Males fed more often on dipteran larvae (more than 66% of all diet items in both habitats), a prey that was primarily buried in the substrate (McNeil et al. 1995), whereas females fed equally on this insect group and bivalve mollusks and copepods, the latter two items occurred primarily on the surface (McNeil et al. 1995). A study on foraging oystercatchers in Australia suggested that repetitive hammering (or probing) was used to capture hard-shelled prey such as crustaceans, bivalves, and gastropods (Lauro and Nol 1995). In our study the prey items were too small to associate with a particular foraging method and this link could only have been accomplished if we had been able to obtain a longer record of the foraging behavior of the birds prior to defecation. The repetitive hammering into the substrate that we observed in as many as 35% of all foraging events may have caused the slight bill reduction in females as a result of greater wear (Hulscher 1985).

Our findings on substrate preference support previous observations on migrating Semipalmated Plovers by Recher (1966) and Burger and coworkers (1977), who found that plovers tended to spend equal amounts of time on damp and wet mud, while largely avoiding dry areas and areas submerged by water. We found no difference in the substrate preference of male and female Semipalmated Plovers, nor did we find a difference in the distance that males and females foraged from the waterline. Therefore, we also rejected the hypothesis that the minor differences in toe length between the sexes were related to differential preference for substrate wetness. The strong site effect we observed in distance to the waterline reflected the steeper slope of the mangrove site with its smaller moist and wet zone. The reason for the sexual dimorphism in this character remains unknown but may be related to differences between the sexes in migratory behavior, of which little is known. Sexes have never been identified in migratory flocks.

Semipalmated Plovers tend to form loose, conspecific foraging aggregations and were generally not observed foraging alone. This behavior and the absence of any overt intraspecific aggression suggest that there is little aggressive behavior on the wintering grounds in early fall. This agrees with other observations from northern Venezuela (Morrier and McNeil 1991), but contrasts with observations from coastal Peru at the end of the overwintering period, in late March, when intraspecific competition might be expected as food resources are depleted (Myers and McCaffery 1984). The diet partitioning that we documented is presumed to have arisen during a period when food resources were limited (Shine 1989).

The open bay mudflats apparently contained more of the fly family Canacidae as indicated by their much greater abundance in fecal samples from both males and females from this habitat. This family is almost exclusively restricted to tidal habitats (McAlpine et al. 1990). By contrast, bivalve mollusks were more common in the feces of birds foraging in the mangrove site. Given the differences that we observed in numbers of items in fecal samples of birds foraging at the two habitats, there may also be important energetic consequences of this variation in habitat quality (Goss-Custard et al. 1991, Tsipoura and Burger 1999).

Previous researchers of the prey community in coastal Venezuela employed sampling methods that selected only items longer than 1.0 mm (Robert and McNeil 1989, Mercier and McNeil 1994, McNeil et al. 1995). Many of the whole food items in the fecal samples we collected were less than 1 mm, indicating that estimates of available prey for Semipal-

mated Plovers (and probably some of the smaller sandpipers) must include these size ranges. Baker (1977) found an average prey size of 5 mm in stomach samples of Semipalmated Plovers collected on the Arctic breeding grounds. The abundance of bivalves and copepods in the samples we analyzed in the range of 0.5 mm suggests a mean prey size of smaller than 5 mm at our site, although this conclusion awaits further work on reassessing prey abundance at this overwintering site.

ACKNOWLEDGMENTS

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